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DISTRIBUTION OF OHIO ANIMALS[1]

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Ohio has a very rich and diversified fauna, as might be expected, in view of the wide range of habitats fringing the glacial boundary. This large complex of species has diverse sources of origin and represents migrations during a number of periods from the Tertiary to the present.

The various elements may be roughly listed as follows: (1) Alleghany Plateau species, (2) boreal relicts, (3) invaders from the Atlantic seaboard, (4) immigrants from south and southwest of the glacial boundary, (5) invaders from the west during the Xerothermic Period, and (6) species which have extended their range as a result of occupation of the land by Europeans. This classification is undoubtedly over-simplified.

The study of the distribution of organisms is by no means a simple matter. Biogeography is admittedly still in its infancy. The climatic regimes of even so short and so recent a period as post Wisconsin time have been subject to violent fluctuation. Deevey (1949, p. 1356) lists five climatic periods since the retreat of the ice, based upon the analysis of fossil pollen in bogs: (1) a cool period, characterized by spruce and fir pollen (2) warmer and dry, with pine pollen conspicuous (3) warm (and moist) with a predominance of beech and hemlock (4) warm and dry, with a maximum of oak and hickory, a period often called the Xerothermic, and (5) the present, cooler and moister, with spruce returning in some northern states.

The Alleghany Plateau fauna contains many species of ancient origin. Transeau (1941, p. 210), Braun (1951), Wolfe (1951) and other students have expressed the opinion that certain elements of the preglacial forests may have existed throughout the Pleistocene in the Plateau within a short distance from the glacial boundary. If such is the case, and I am sympathetic with this viewpoint, it would seem to follow that some of the Pliocene animals were also present throughout the Ice Age.

Biologists are not in agreement on this point. The most extreme view to the contrary is that of Deevey (1949, p. 1375) who, after a very extensive survey of the biogeography of the Pleistocene, comes to the conclusion that glacial chilling must have been so extensive that warmth-loving species of plants and animals could have survived only in peninsular Florida and in Mexico. Potzger (1951) has summarized the evidence of northern plants and animals in the southeastern states during the Pleistocene: spruce pollen has been reported from Texas, Louisiana, Florida and North Carolina; remains of Musk-ox, a species now known only from the Arctic,

[1]Presidential address at the annual meeting of The Ohio Academy of Science at Miami University, Oxford, Ohio, on April 5, 1951. It is somewhat modified and expanded from a paper, "Animal Distribution in Relation to the Glacial Boundary" which was part of a symposium on "The Glacial Border" presented before The Ecological Society of America at Columbus, Ohio, on September 13, 1950.

have been recorded from Mississippi and Oklahoma, while the woolly mammoth has been reported from Texas and Florida.

Some of these records may very likely be fossil flotsam, as Wolfe (1951) has suggested. Others of the reports are from the coastal plain. As Braun (1950,

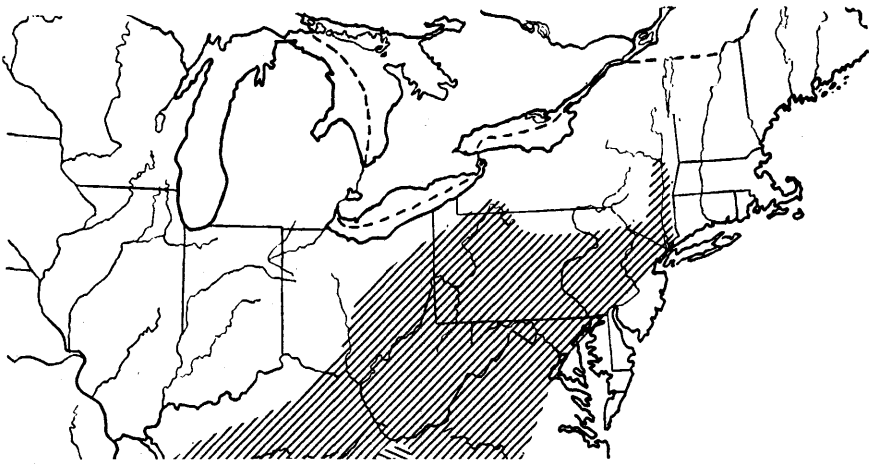

FIGURE 1. Distribution of the red salamander. From Bishop, 1943.

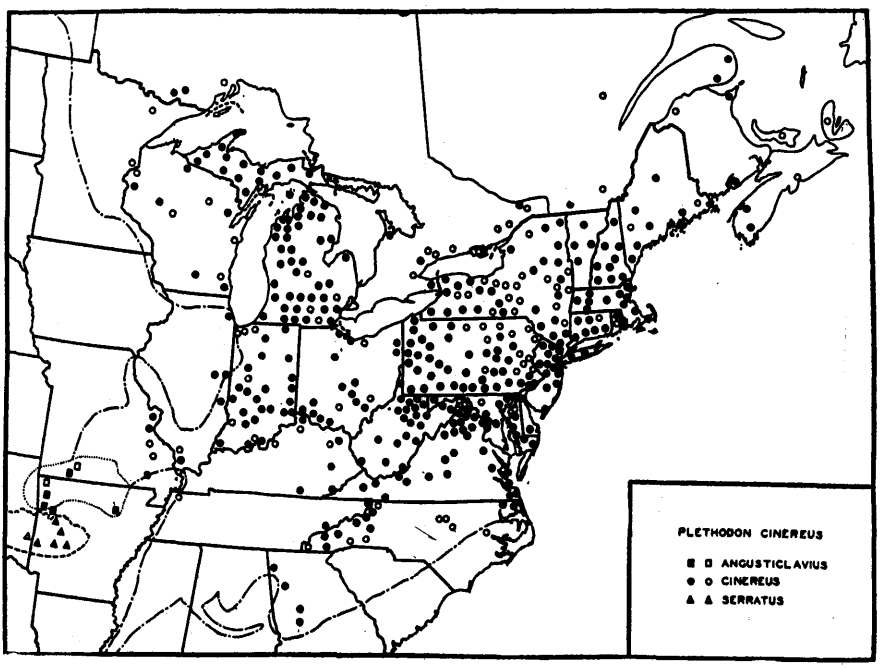

FIGURE 2. Distribution of the red-backed salamander. From Grobman, 1944.

p. 513) indicates, during the maximum of the Wisconsin, the level of the ocean was lowered by many feet, exposing vast areas of coastal terraces. These, and the extensive fluviatile deposits in consequence of the tremendous floods of glacial

water, may well have been occupied temporarily by coniferous forests and boreal bogs and the northern animals associated with them.

But even if we should concede that many northern plants and animals were able to penetrate far into the southeastern states during the Pleistocene, I do not believe that the converse necessarily follows, namely that many of the so-called southern animals could not have survived close to the glacial border. Granting the potent ability of many organisms to extend their ranges rapidly for great distances, nevertheless there are many other species which I can not believe were capable of migrating in a few thousands of years from Ohio to Florida or Mexico and back again. While it is perfectly true that an animal may have legs and perhaps wings and hence be physically capable of rapid and extensive migration, it is also

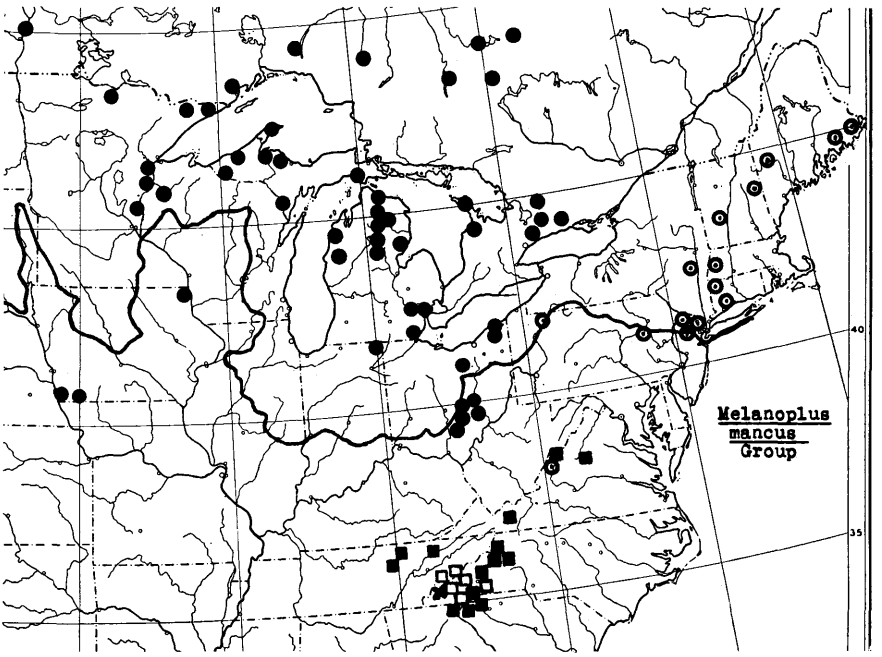

FIGURE 3. Distribution of the *Melanoplus mancus* group of grasshoppers. Solid circles, *M. islandicus;* open circles, *M. mancus;* solid squares, *M. celatus;* open squares, *M. divergens;* "X," *M. serrulatus*. Heavy line indicates Wisconsin boundary.

an axiom that an animal can not successfully extend its range beyond its suitable habitat and to that extent can expand into new territory no more rapidly than a plant. Both must await suitable ecological conditions before moving into them.

It is freely conceded that our knowledge is still fragmentary on the subject. Clarification must await much more evidence than we now possess. It is freely conceded, as Dr. Deevey observes, that the present range of an animal does not indicate that it has always been there. Nevertheless, the distribution patterns and the ecological requirements of many animals in the middle west seem to me to indicate that they survived the Wisconsin glaciation close to the glacial boundary. I believe that this is true, not only in the unglaciated Plateau, but also *within glaciated territory*. A number of examples will be offered in support of this opinion as we proceed.

A great many Plateau species have been unable to extend their range into glaciated territory, while others have spread widely to the north and west. This is strikingly illustrated by the Plethodont salamanders. This family of lungless

salamanders is of ancient origin, having originated, Dunn (1926) believes, in the Southern Blue Ridge mountains, from which center the family has dispersed widely throughout the United States. Some of the more northern of the Plateau species are still closely confined to the unglaciated Plateau, such as *Plethodon wehrlei*, the Green Salamander, *Aneides aeneus*, and the Red Salamander, *Pseudotriton ruber* (fig. 1). As contrasted with these, the Red-backed Salamander, *Plethodon cinereus*, has extended its range as far north as Minnesota and New Brunswick, possibly as far north as Hudson's Bay (fig. 2). Grobman (1944) estimates that this small salamander may in its spread have averaged as much as 1 mile every 37 years since the time of the Cary substage of the Wisconsin glaciation. He points out, however, that in the event that Cape Breton Island and the Gaspe Peninsula

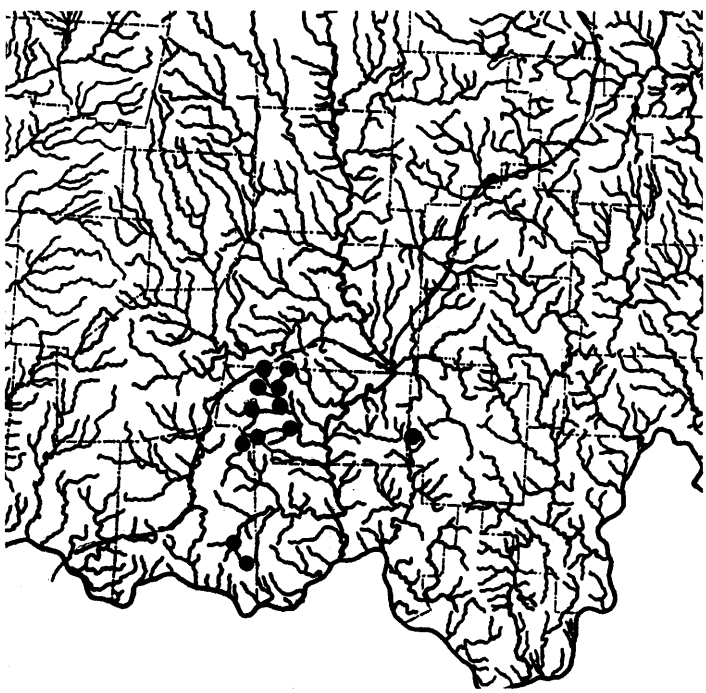

FIGURE 4. Ohio distribution of the minnow, *Clinostomus vandoisulus*. (M. B. Trautman, ms.)

were not glaciated by the Wisconsin ice, these areas, along with the driftless area of Wisconsin might well have been auxiliary dispersal centers, in which event the speed of dispersal would have been considerably less. On the other hand, recent Carbon 14 findings indicate a much shorter period since Cary time than was previously believed, which would increase the assumed speed of dispersal. It seems probable that a westward dispersal of *cinereus* from its original home in the Plateau took place prior to the Wisconsin glaciation, and that during Wisconsin time it survived over a wide area along the southern periphery of the ice front, whence it quickly returned to the north following the retreat of the ice.

The grasshoppers of the Mancus group of the genus *Melanophus* present a distributional picture which is strikingly similar (fig. 3). These short-winged (and hence flightless) grasshoppers are known only from the eastern United States, three species being confined to the southern portion of the Appalachian Highland. One species, *Melanoplus mancus*, is restricted to the northern portions of the

mountains, from which it has spread a short distance into glaciated territory. The fifth species, *Melanoplus islandicus*, has spread widely to the northwest. *Islandicus* thus has a pattern in the middle west similar to *Plethodon cinereus*. It is my belief that it had dispersed widely from its place of origin in the Plateau prior to Wisconsin times. The Wisconsin ice sheet may have all but exterminated the species, but small populations in one or more refugia enabled it to repopulate a large area of glaciated country after the retreat of the ice. The distribution of *mancus* also indicates to me that this species survived the Wisconsin not far south of the boundary.

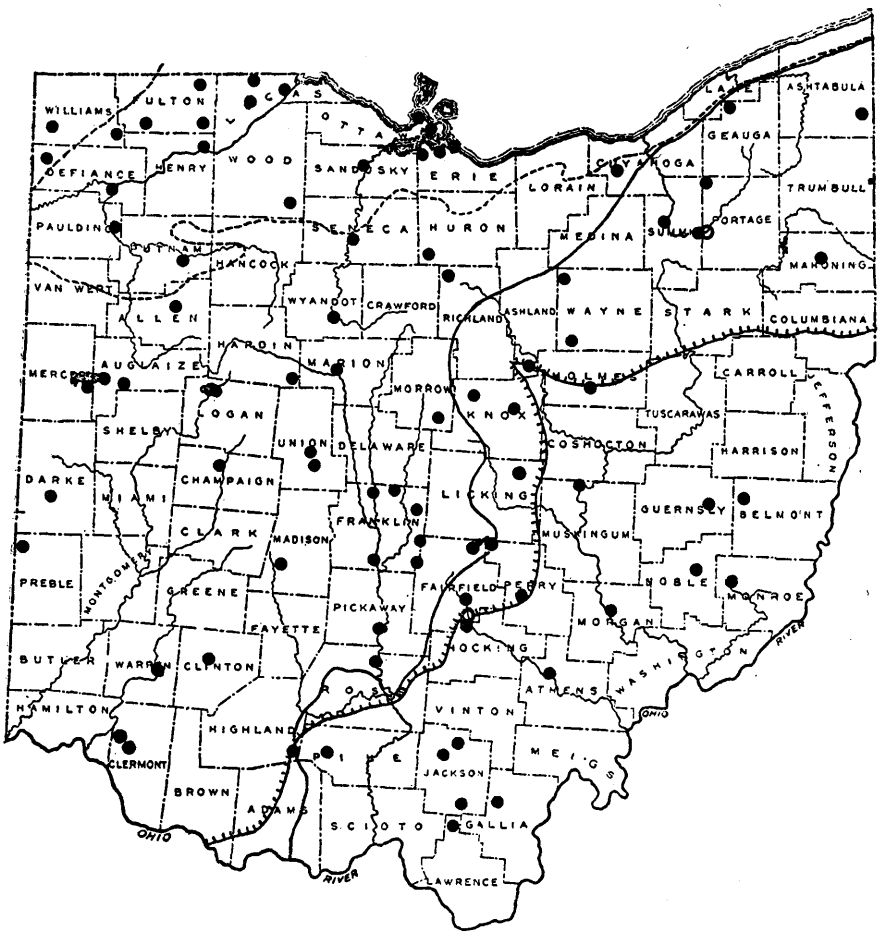

FIGURE 5. Ohio distribution of the striped chorus-frog. From Walker, 1946.

Another example of a southern species which has not been able to invade glaciated territory is presented by the Rosy Dace, *Clinostomus vandoisulus* (fig. 4). In Ohio, this handsome, little minnow is restricted to the headwaters of a few small tributaries of the preglacial Teays river system.

I agree with Milton Trautman (1951) that the distribution of *vandoisulus* suggests a relict population of long residence, probably since preglacial times. The Ohio River, which came into existence when an early glacier blocked the path

of the northward-flowing Teays, would seem to be an effective barrier to the spread of this minnow. It is a fish of small, clear, cool, headwater streams. While it would, of course, be physically possible for it to swim across a much larger river than the Ohio, all the evidence indicates that it strictly avoids warm, sluggish, silt-laden waters. I believe that its distribution pattern in Ohio indicates that it has survived all three glacial periods of the Pleistocene practically in situ.

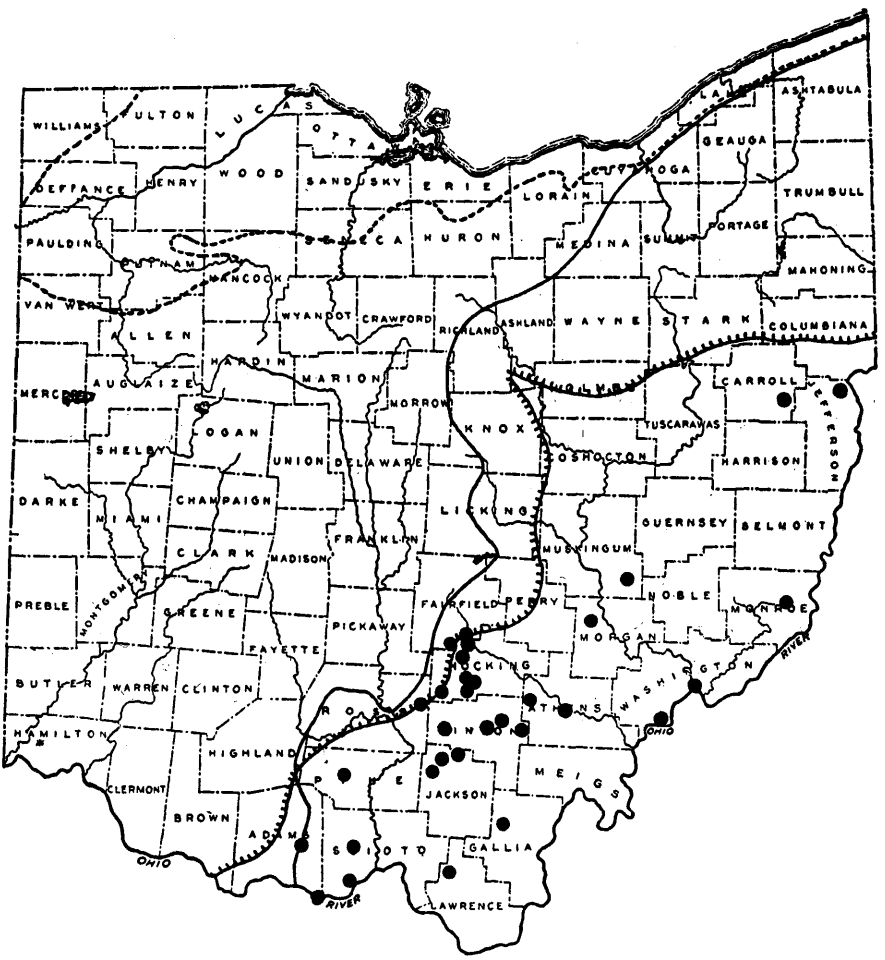

FIGURE 6. Ohio distribution of the upland chorus-frog. From Walker, 1946.

A considerable portion of the unglaciated Plateau along the glacial border has been dissected by an intricate network of filled valleys of preglacial and interglacial streams. These have been filled sometimes with many feet of lake silts and outwash. In some cases, glacial outwash is plastered high up on the adjacent valley walls, and in many cases limestone outwash has been washed many miles into a Plateau consisting largely of acid sandstones. While the mature uplands of the unglaciated Plateau are noteworthy for their lack of swamps and ponds, these are plentiful in the poorly drained filled valleys.

As a result, some of the filled valleys support a flora and fauna vastly different

from that of the unglaciated uplands, in many cases resembling that of the glaciated till plains. And whereas the preglacial valleys were often important migration routes for plants and animals from the south and southeast during pre-Pleistocene times, we now see a reverse migration taking place over the same valleys, since the filled valleys now serve as invasion routes for many species from the west which otherwise have been unable to penetrate the unglaciated Plateau. The striped chorus-frog, *Pseudacris triseriata*, is a conspicuous example (fig. 5). *Triseriata* is a western form, ranging as far west as Idaho and Arizona. It has, in comparatively recent times extended its range eastward along the Lake Plains to Oswego, N. Y. and it is widespread in the unglaciated Plateau of eastern Ohio, where it is restricted to filled valleys. The small spring pools of the unglaciated uplands are

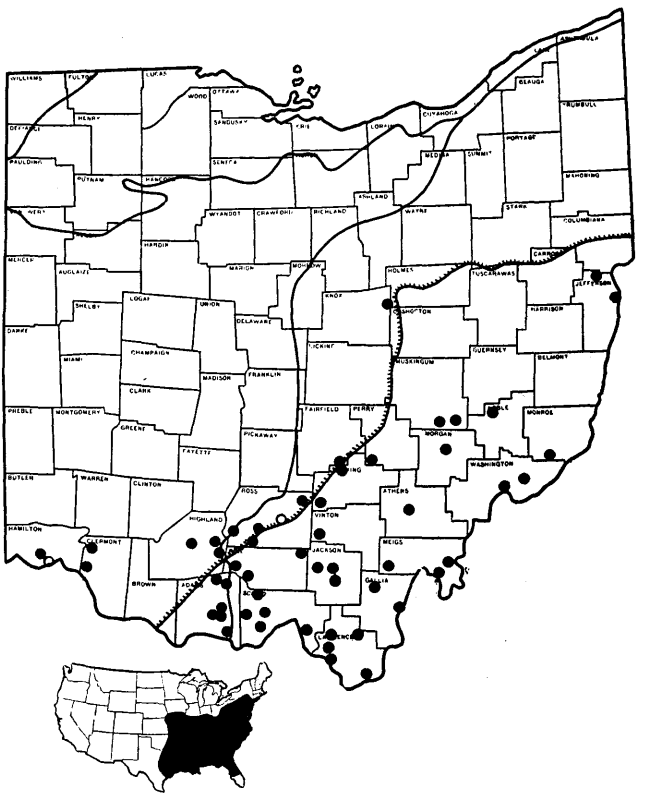

FIGURE 7. Ohio distribution of the fence lizard. From Conant, 1938.

utilized by *Pseudacris brachyphona*, an ancient and more primitive form. *Brachyphona* has not been able to spread beyond the unglaciated Plateau and I think that it is not too unreasonable to believe that it existed throughout the Pleistocene somewhere close to its present range (fig. 6).

The boreal element of our Ohio fauna is found mostly in the boreal relict bogs which occurred abundantly in the Wisconsin drift at the time of the arrival of the white man in America. Such bogs are rare or absent in the Illinoian drift and the border of the unglaciated Plateau, except in filled valleys. The bogs are rich in boreal animals, and since many of them lie adjacent to the unglaciated Plateau, the glacial border therefore presents the unusual picture of Canadian animals occurring in close proximity to animals of southern latitudes.

Among the numerous northern animals to be found in boreal relict bogs may be mentioned the Wilson's thrush, northern water-thrush, swamp sparrow, rose-breasted grosbeak, red-backed vole, woodland jumping mouse, the grasshopper, *Melanoplus borealis*, the copper butterfly, *Lycaena epixanthe* and the deer-fly *Chrysops frigida*.

While there are a limited number of relict plants of the Hemlock-Hardwoods forest in deep gorges in some portions of the glacial border, the northern fauna is poorly represented in such situations, due, possibly to their restricted area.

In early post-Wisconsin time, a considerable migration of Atlantic coast flora and fauna took place into the Great Lakes region possibly along the Hudson-Mohawk glacial outlet. Peattie (1922) has discussed the plants which took part in this invasion, but the animals accompanying them are not so well known. The migration consisted of two distinct elements: (1) Xerophilous plants and animals which presumably followed the sand and gravel outwash plains and which

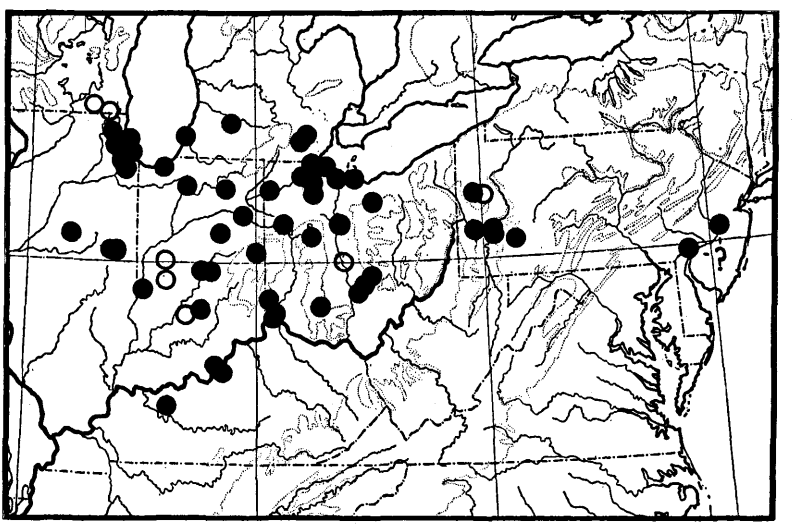

FIGURE 8. Distribution of Kirtland's water snake. From Conant, 1943.

have survived in sandy situations around the Great Lakes and, (2) Hydrophilous flora and fauna which may have migrated by way of the swales and marshes along the same route.

Representative examples of the first category consist of the beach grasshoppers, *Trimerotropis maritima* which is widely distributed on sand dunes along the southern Great Lakes and the rarer *Psinidia fenestralis*. Another eastern grasshopper, *Scirtetica marmorata* is found in open sandy or rocky woodland.

The hydrophilous element from the Atlantic coastal plain seems to have survived largely in alkaline bogs, which apparently provide ecological conditions similar enough to those of the salt marshes and brackish situations of the Atlantic coast to have permitted the survival of this relict element for 10,000-odd years. That this flora and fauna may have been quite extensive in former times is indicated by the fact that isolated relicts occur in marl bogs at the foot of terminal moraines of the Wisconsin, 150 miles or more from Lake Erie.

A large group of Ohio animals consists of those which apparently existed in refugia just beyond the ice boundary to the south and southwest during the Wisconsin times. As with the Plateau fauna, a number of southern species have never been able successfully to invade glaciated territory, the northern boundary

of their range in some cases practically coinciding with that of maximum glaciation, or, in some cases, the Wisconsin terminal moraines. The range of the fence lizard or common swift *Sceloporus undulatus*, seems to follow this pattern (fig. 7)as do those of the cave salamander, *Eurycea lucifuga*, and the king snake, *Lampropeltis getulus*.

Many other species, of course, have invaded the glaciated territory far to the north. Some of these are known only from the middle west and may be considered middle-western endemics.

Kirtland's water snake, *Natrix kirtlandii* is a case in point (fig. 8). This small, secretive water snake is endemic to the eastern portion of the prairie peninsula, where it is practically confined to glaciated territory. To me, its distribution

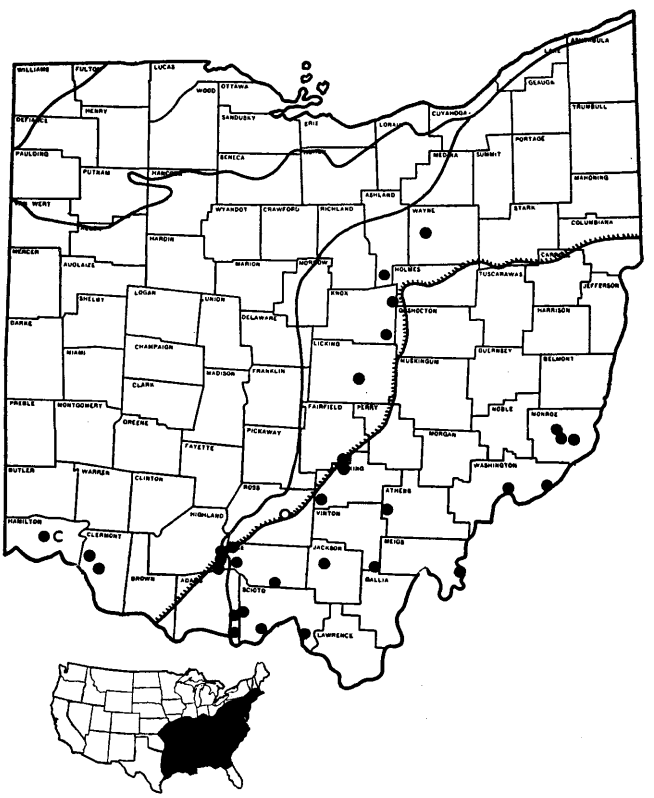

FIGURE 9. Ohio distribution of the copperhead snake. From Conant, 1938.

pattern suggests that it survived the Wisconsin glaciation somewhere close to the ice-front, spreading northward after the retreat of the ice. Unlike the prairie species it is not known west of central Illinois. If it retreated to Florida during the Wisconsin and subsequently returned to its present range, it has left no known relict colonies along the route, nor is there evidence that it can survive in unglaciated terrain. Two similar examples will be discussed later.

The Xerothermic period resulted in the invasion of a large element of prairie plants and animals. Schmidt (1938) has given an excellent account of the reptiles and amphibia of the Prairie Peninsula. To the examples listed by him may be added the plains garter-snake, *Thamnophis radix*, which has recently been found as

an isolated prairie relict as far east as central Ohio. Among the mammals, the badger and its favorite prey, the 13-lined spermophile are members of the prairie fauna which are known as far east as Ohio, while a great many prairie birds and insects accompanied the invasion of prairie plants eastward.

The occupation of North America by Europeans has resulted in the most radical change in the flora and fauna in a shorter period of time than any known phenomenon in the region under consideration. The clearing of the timber and the subjugation of the land to agriculture have converted a cool, moist habitat into a hot dry one. At the same time, every farm has become an artificial prairie. Radical changes have taken and are taking place in our fish populations, as Milton Trautman (1951) has shown. Fish species which require clear water have been

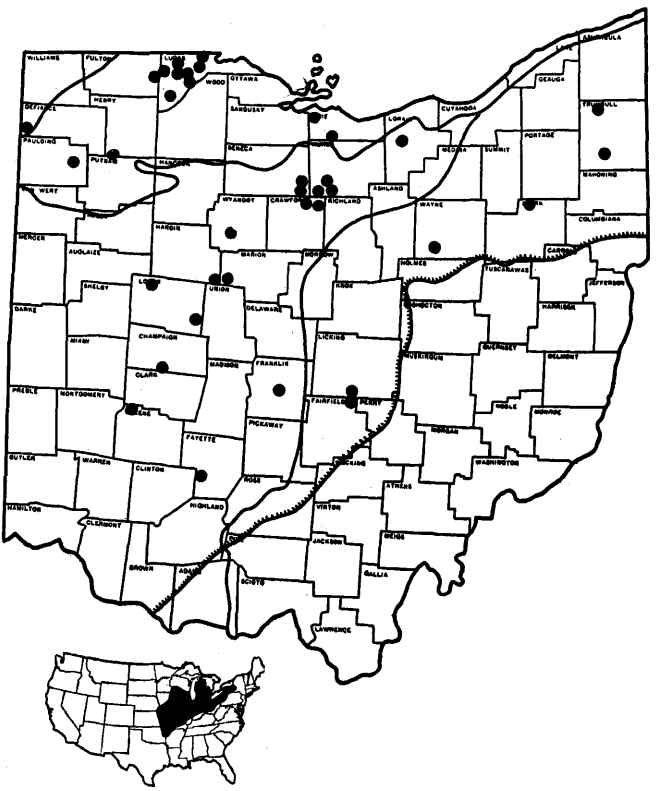

FIGURE 10. Ohio distribution of the massasauga. From Conant, 1938.

extirpated or decimated in numbers and are being replaced by those species which can tolerate a heavy concentration of silt from our corn fields.

Southern birds, such as the cardinal, Bob-white, tufted titmouse and the mockingbird are extending their range to the north. Birds and mammals of prairie-like habitats, such as the meadowlark, vesper sparrow, bobolink, prairie white-footed mouse and the fox squirrel are replacing birds and mammals of the forest. The small-mouthed salamander and the striped chorus-frog are increasing at the expense of such animals as Jefferson's salamander and the wood frog.

Perhaps the most dramatic invasion by a prairie animal has been that of the prairie horned lark, which has overspread the northeastern United States within the last 80 years (Pickwell, 1931). Its exact range at the time of the westward

influx of white settlers will probably never be known. Audubon knew nothing of nesting horned larks in the middle west.

The Xerothermic Period could not have failed to favor this bird and it very possibly enjoyed a wide eastern range at that time. However, it can not exist in tall-grass prairie any more than it can in forest. It requires sparsely vegetated habitats with short and scant ground-cover. At the time of the settlement of the middle-west, it may well have existed in scattered refugia in sandy areas, as Barrows and others contend. But if so, no evidence to that effect has been produced. While competent bird observers were few and scattered prior to the 1870's, there were enough of them to prove conclusively that nesting horned larks did not exist in certain large areas in the eastern United States where they are now plentiful.

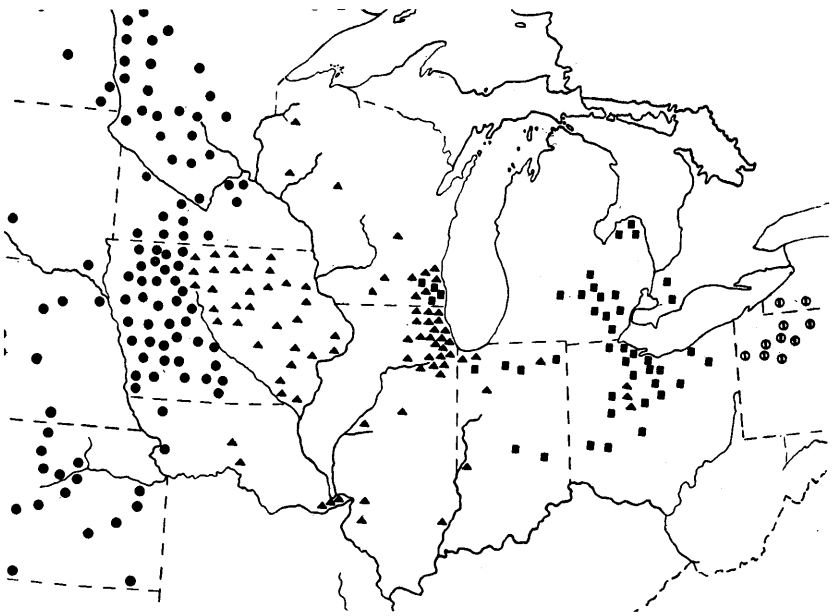

FIGURE 11. Distribution of the *radix* group of garter-snakes. Open circles, *Thamnophis brachystoma;* squares, *T. butleri;* triangles, *T. radix radix;* solid circles, *T. radix haydenii.* From Smith, 1949.

The original range of the prairie horned lark may have been west of the Mississippi, possibly with limited extensions eastward into sandy areas in Wisconsin and Illinois. Coues reported nesting larks in Wisconsin in 1874, and in 1878 Ridgeway reported the birds abundant in suitable localities in Illinois, but these may well represent birds which had invaded from farther west.

The first definite evidence of an eastward invasion was a report by McIlwraith of larks nesting at Hamilton, Ontario, possibly as early as 1871. They were reported for western New York in 1875, for 3 additional localities in that state in 1876 and for Indiana in 1878. There were no records for Ohio when Dr. John M. Wheaton published his Birds of Ohio in 1880. After 1880, the species spread rapidly and now nests commonly over most of the northeastern United States and adjacent parts of Canada.

The general rule that it is the southern species which have increased their range with the destruction of the forests is subject to a number of exceptions in which northern animals have spread southward. The savanna sparrow and the

least weasel are examples and I believe the same to be true of the red fox, *Vulpes fulva.*

The case of the red fox is as remarkable as that of the lark but less well documented. Early settlers were almost unanimous in the belief that the red fox was absent from eastern North America until it was introduced from England for the purposes of sport. This belief, of course, did not take into account the fact that the European and our red fox are considered distinct species and further that the red fox group is widely distributed in northern North America, with a number of species and races, indicating long residence in the nearctic region.

There is little doubt, however, that *fulva* was a rare animal before the land was cleared by Europeans. The Ohio State Museum has a large quantity of animal bones from late prehistoric Indian village sites of the Fort Ancient culture. We have found as yet no unquestioned bones of red fox, though remains of gray

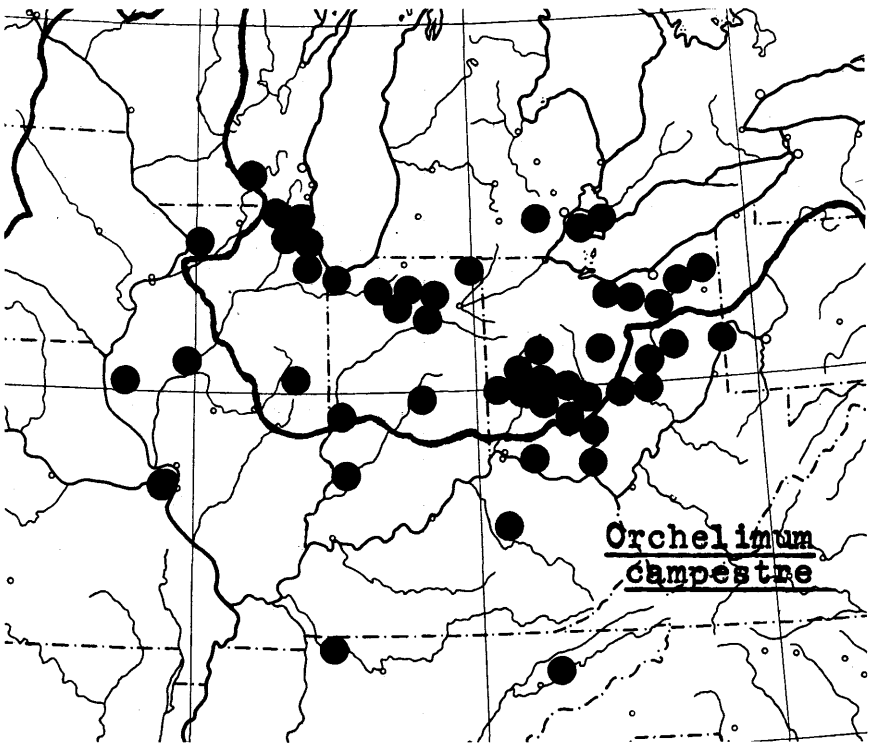

FIGURE 12. Distribution of the grasshopper, *Orchelimum campestre.* Heavy line indicates Wisconsin boundary.

fox (*Urocyon*) are plentiful. The red fox, like the savanna sparrow and the least weasel, already mentioned, is an animal of open country, while the gray fox is a woodland animal.

The fact that all the other North American species of the *Vulpes fulva* group are either northern or high mountain forms, may indicate that *fulva* also had a northerly range in pre-Columbian times, from which it spread southward and southeastward with the clearing of the forests.

It will thus be seen that climatic and cultural changes have resulted in the juxtaposition in our State of many varied faunas. I will conclude with a few striking examples.

Three species of moles of diverse origin occur along the glacial border. The star-nosed mole exists as a northern relict in relict bog habitats. The hairy-tailed mole is an Appalachian species which has never been able to extend its range more than a few miles west of the Plateau, while the Prairie Mole occupies all of the territory west of the Plateau and is apparently extending its range eastward.

The copperhead snake and the massasauga also occupy reciprocal habitats. The copperhead is so closely confined to unglaciated territory and the Illinoian drift that the northern limit of its range virtually presents a picture of the Wisconsin boundary (fig. 9). The massasauga on the other hand is restricted to wet prairie, or prairie-like habitats in the Wisconsin drift and its range closely parallels the Prairie Peninsula (fig. 10).

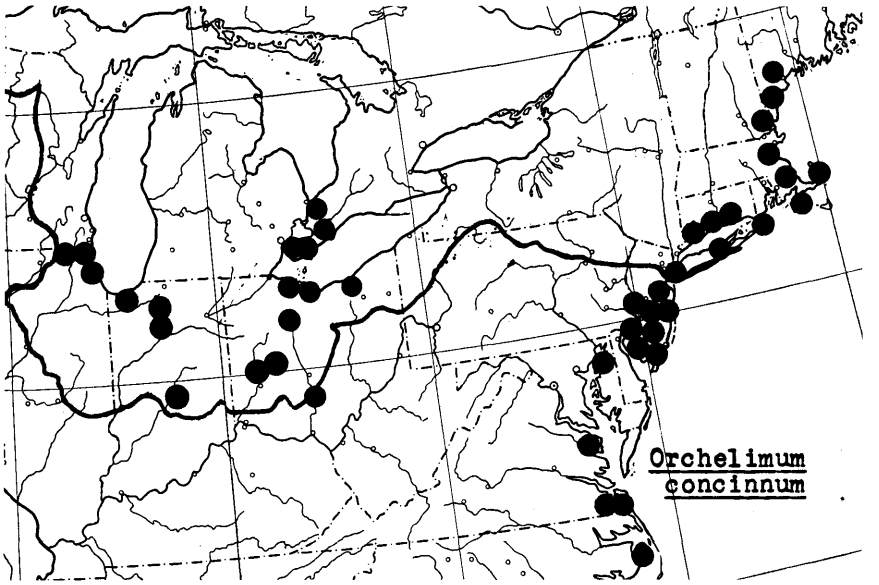

FIGURE 13. Distribution of the grasshopper, *Orchelimum concinnum*. Heavy line indicates Wisconsin boundary.

The garter snakes of the *radix* group provide an interesting distributional picture (fig. 11). *Thamnophis radix* is a western form, existing, I believe, as an isolated prairie relict of the Xerothermic Period as far east as Ohio. *Thamnophis butleri* like Kirtland's water snake, already noticed, is an endemic of the eastern portion of the Prairie Peninsula. Its distribution pattern seems to me to indicate that, like *kirtlandii*, it existed in refugia within glaciated territory during Wisconsin time, spreading northward after the retreat of the ice (Conant, Thomas, and Rausch, 1945). *Thamnophis brachystoma* is restricted to a small area in the unglaciated uplands of northwestern Pennsylvania and southwestern New York. Unlike *butleri*, it has been unable to invade glaciated territory for any great distance. I agree with Netting (*in* Conant, 1950, p. 76) in the opinion that it is undoubtedly a pre-Wisconsin relict, and that it may well have survived throughout the Wisconsin not far from its present range.

Possibly the most striking picture of all is provided by the distribution of three grasshoppers of the *Orchelimum concinnum* group. These three are so closely related that Orthopterists currently recognize only one species with two geographic races, considering the third form an absolute synonym. I consider the three

distinct species, since they exist together in a number of places without evident intergradation.

Orchelimum campestre is another of the middle western endemics and is widely distributed in marshes throughout the Wisconsin drift, into which, I believe, it spread from refugia not far from the ice front (fig. 12). *Orchelimum concinnum* is abundant along the Atlantic seaboard, but it exists as a relict species in marl bogs and other alkaline marshes in the southern portion of the Great Lakes region (fig. 13). There is little question but that it spread into the latter area from the Atlantic coast in early post-Wisconsin times. The third species, *Orchelimum delicatum* has a wide range west of the Mississippi, but it exists eastward as a relict of the Xerothermic period in a few grassy swales, mostly those adjacent to sand dunes (fig. 14).

Speciation in this group has apparently taken place as a result of isolation during the Pleistocene, after which the strange vagaries of climate enabled the three forms again to come in contact along the glacial border in the middle west.

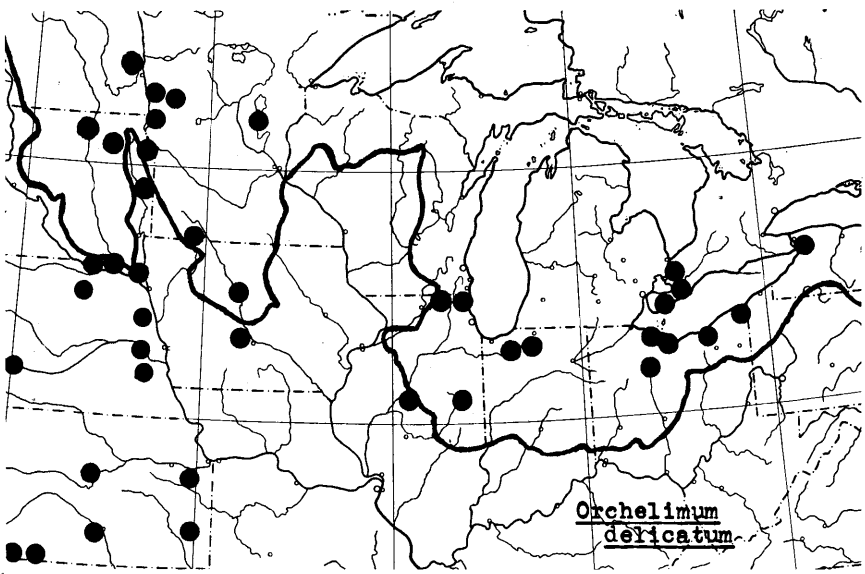

FIGURE 14. Distribution of the grasshopper, *Orchelimum delicatum*. Heavy line indicates Wisconsin boundary.

I hope that the brief sketch which I have presented will illustrate the wealth and diversity of the Ohio fauna, as well as the complexity of its sources of origin, both in time and space. The distribution and the ecology of many Ohio animals, I believe, raises a strong presumption that they survived the Wisconsin or perhaps the entire Pleistocene close to the glacial border, some species in refugia within the limits of glaciated territory.

The problem is so complex and concrete evidence as yet so meagre, that many of my interpretations may be incorrect. Very possibly all of them are. If so, perhaps this paper may stimulate some other worker to uncover evidence which will provide us with a more accurate picture.

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